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LIVESTOCK DUNG AS A FOOD RESOURCE AND THERMAL REFUGE FOR RANGELAND GRASSHOPPERS (ORTHOPTERA: ACRIDIDAE)

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Abstract.—Fourteen species of grasshoppers from three subfamilies of Acrididae were observed feeding on dry cattle and horse dung at two rangeland sites in southwestern Montana. While feeding within dung cavities during the middle of the day, they attained equilibrium body temperatures well below the critical thermal maxima typically observed for grasshoppers. The implications of these observations for studies of grasshopper diet and nutrient cycling on rangeland are discussed.

Key Words.—Insecta, thermoregulation, manure, decomposition, rangeland, grasshopper

Grasshoppers play a role in ecosystems beyond that of primary consumers of living plants. They reduce forage available to other animals by clipping, but not consuming standing vegetation (Hewitt & Onsager 1983). They are also scavengers upon insect cadavers (Lockwood 1988, O'Neill et al. in press) and dead plant matter (personal observation). In anecdotal accounts, their omnivory extends to an amazing variety of materials during outbreaks, including clothing, curtains, upholstery, rake handles, rubber, tree bark, and human flesh (Shotwell 1958, Gangwere 1961). This paper presents observations of feeding by grasshoppers on cattle and horse dung, and discusses the potential implications for grasshopper diet studies and for rangeland nutrient cycling. In addition, to determine whether the grasshoppers could use dung cavities as thermal refuges during hotter times of day, I measured environmental temperatures and grasshopper operative body temperatures outside and inside of dung cavities.

Materials and Methods

This study was conducted from 15 Jul through 2 Sep 1992, primarily at two sites. One area was 1 km N of Logan, Montana (latitude 45°45′N, longitude 111°35′W), and had native vegetation characterized by the grasses *Stipa comata* Trinius & Ruprecht and *Bouteloua gracilis* (Humboldt, Bonplan, & Kunth) Lagasca y Segura ex. Steudel. The site is lightly grazed by horses, although none were present during observations. The other area ("red barn site") was 11.5 km SSW of Three Forks, Montana (and 18 km SE of the Logan site). Observations were also made at a third site ("dead cow pasture") 8 km S of Three Forks. The native vegetation at both Three Forks sites is the same as at the Logan site, but both areas have been plowed and reseeded with crested wheatgrass, *Agropyron cristatum* (L.) Gaertner and alfalfa, *Medicago sativa* L. Both sites are grazed by cattle, but cattle were not present when observations were being made.

The identity of grasshoppers feeding on dung was determined at undisturbed dung masses and at those where I had broken open the hardened and dried surface crust to expose the darker and somewhat more friable material within. The latter method allowed me to increase the sample size of feeders over a shorter period of time. Feeding grasshoppers were distinguished from those simply resting on or within the dung. To determine grasshopper community composition, two to four hundred 180° arc sweep samples were taken on several days in each area. Samples were returned to the lab and frozen until the frequency distribution of species, developmental stages, and sexes could be recorded.

Temperatures of soil and dung surfaces (T_S) were measured to the nearest 0.1° C with copper/constantan thermocouples and a Cole-Parmer thermocouple thermometer. T_S was measured with the tip of the probe shaded from direct solar radiation. Operative body temperatures (T_E) (Tracy 1982) were measured by inserting the tip of a thermocouple (wire diameter = 0.25 mm) posteroventrally into the enter of the thorax of dead *Melanoplus sanguinipes* (Fabr.), which were then dried before being used in the field. The T_E of the grasshoppers was then determined in two locations: on fully insolated soil surfaces outside of the dung cavities and in the shaded confines of cavities in which grasshoppers had been observed perched within the previous 2 min. Comparisons of T_S or T_E from different locations were made using Wilcoxon signed-ranks tests.

Results

At the red barn site, 15 species of Acrididae were either collected in sweep samples or observed in the habitat (Table 1). Among the species present in a 200 sweep sample (n = 488 grasshoppers) taken on 29 Jul, the following species predominated: *Aulocara elliotti* (Thomas) (51.2% of sample), *Ageneotettix deorum* (Scudder) (17.2%), *M. sanguinipes* (11.6%), *M. infantilis* (Scudder) (7.2%), and *Phoetaliotes nebrascensis* (Thomas) (5.3%). At the Logan site, 17 species were present (Table 1), with the following species in the greatest abundance in a 200 sweep sample (n = 245 grasshoppers) taken on 27 Jul: *Psoloessa delicatula* (Scudder) (all 1st and 2nd instar nymphs, 55.1%), *A. deorum* (15.9%), *M. infantilis* (10.6%), *M. sanguinipes* (4.9%), and *Amphitornus coloradus* (Thomas) (3.2%).

It is not known when the dung at the two sites was deposited. However, both the cattle and horse dung were gray with a somewhat weathered and bleached appearance on the outside, and dark brown, dry, and friable with little moisture present inside.

When I broke open cattle dung at the red barn site, grasshoppers typically began arriving and feeding on the newly exposed inner material within 10 minutes. At undisturbed dung (i.e., that not tread upon by large vertebrates), they usually fed within cavities in the dung that were presumably created by the grasshoppers themselves. Many of the dung piles were hollowed out due to grasshopper feeding and some eventually collapsed, so that only dried fragments of the surface crust remained. Unlike cattle dung, horse dung is deposited in piles of individual egg-shaped pieces. The result of feeding by grasshoppers on these pieces was quite distinctive. Like the cattle dung, the horse dung was often hollowed out and even burrowed through and the surface on which feeding occurred was relatively smooth due to even clipping by the grasshoppers' mandibles. Dung on which extensive feeding had occurred also had large deposits of grasshopper feces. These were particularly extensive beneath hollowed out cattle dung, where a large mat of grasshopper feces up to one cm deep sometimes accumulated.

Evidence of grasshopper feeding on dung was extensive at all three sites. Of 50

Table 1. Grasshopper species present in the communities of the two research sites and observed feeding on cattle (red barn site at Three Forks) or horse (Logan) manure.

Species	Red barn site		Logan site		Feeding category[a]
	Present	Feeding	Present	Feeding	
Gomphocerinae					
Acrolophitus hirtipes (Say)	−	−	+	−	F
Aeropedellus clavatus (Thomas)	−	−	+	−	G
Ageneotettix deorum (Scudder)	+	+	+	+	G
Amphitornus coloradus (Thomas)	+	+	+	+	G
Aulocara elliotti Thomas	+	+	+	+	G
Phlibostroma quadrimaculatum (Thomas)	−	−	+	+	G
Psoloessa delicatula Scudder (nymphs)	+	−	+	−	G
Oedopodinae					
Arphia pseudonietana (Thomas)	+	−	+	+	G
Camnula pellucida Scudder	+	+	−	−	G
Dissosteira carolina Saussure	−	−	−	−	MH
Encoptolophus costalis Scudder	+	+	+	−	G
Hadrotettix trifasciatus (Say)	−	−	+	−	MH
Hesperotettix viridus (Scudder)	−	−	+	−	F
Metator pardalinus (Saussure)	+	+	+	+	G
Spharagemon equale (Say)	+	+	+	−	MG
Trachyrachis kiowa Thomas	+	+	+	+	G
Xanthippus corallipes Haldeman (nymphs)	−	−	−	−	G
Melanoplinae					
Melanoplus bivittatus (Say)	+	−	−	−	MF
Melanoplus infantilis Scudder	+	+	+	+	G
Melanoplus packardii Scudder	+	−	+	+	MH/F
Melanoplus sanguinipes (Fabr.)	+	+	+	+	MH
Phoetaliotes nebrascensis (Thomas)	+	+	−	−	G
Total number of species	17	11	18	10	

[a] Feeding preference, where F = forbivorous, MF = mixed forbivorous, MH = mixed herbivorous, MG = mixed gramnivorous, and G = gramnivorous (classification from Mulkern et al. 1969, with the exception of *A. elliotti, C. pellucida, M. pardalinus,* and *X. corallipes* where designation was based on Capinera & Sechrist, 1982).

undisturbed dung piles surveyed at the red barn site on 29 Jul, 34 showed evidence of grasshopper feeding and 19 had feeding grasshoppers present. On the same day, 30 of 50 undisturbed dung piles surveyed at the nearby dead cow pasture showed evidence of grasshopper feeding and 26 had feeding grasshoppers present. At the Logan site on 27 Jul, 40 of 50 undisturbed piles of horse dung showed evidence of grasshopper feeding and 2 had feeding grasshoppers present. The 50 piles had an average of 3.2 feeding sites (SE = 0.4). Extensive feeding was also observed on 24 individual pieces of horse dung, broken open and placed along a transect on 27 Jul. When I returned to the site on 29 Jul, 20 had been fed on (presumably by grasshoppers), with three having at least 10% missing. By 2 Sep, no others had been fed upon, but I estimated that 11 had at least 25% of the original mass missing and three had at least 50% missing.

Fourteen of the 22 species present at the two sites were observed feeding on dung (Table 1). At the red barn site, the species most commonly observed feeding on cattle dung in 6 days of observation were *A. elliotti* (48.9% of 288 observations), *A. deorum* (24.3%), *M. sanguinipes* (14.9%; included adults and 4th and 5th instar nymphs), *Spharagemon equale* (Say) (4.5%), and *P. nebrascensis* (2.8%). At Logan, those most commonly observed feeding on horse dung in 4 days of observation were *A. deorum* (32.6% of 43 observations), *A. elliotti* (18.6%), *M. infantilis* (14.0%), and *Phlibostroma quadrimaculatum* (Thomas) (11.6%). At this site, I also observed two female *A. elliotti* and one female *Metator pardalinus* (Saussure) feeding on dung while *in copula*. Adults of both sexes of all of these species were observed feeding. The probability that a species was observed feeding on dung was related to its abundance in the community. The number of individuals of a species taken in a sweep sample at the red barn site on 29 Jul was significantly correlated with the number of each species observed feeding on dung at this site on 28 and 29 Jul ($r = 0.97$, $P < 0.0001$, $n = 14$).

Non-feeding grasshoppers were also observed sitting within shaded cavities, atop dung, and in shade next to dung, particularly during hotter periods of sunny days. At Logan on 6 Aug, the surface temperatures of the dung or soil within dung cavities during the afternoon were 19.7° C lower on average than the bare soil surface temperature outside of the cavity (Fig. 1; Wilcoxon test, $P < 0.001$). At the red barn site on 28 Jul, the temperatures within dung cavities were 16.6° C lower on average than the soil surface temperatures outside of the cavity (Wilcoxon test, $P < 0.001$). Similarly, at the same site on 7 Aug, the temperatures within dung cavities were 18.9° C lower on average than the soil surface temperatures outside of the cavity (Wilcoxon test, $P < 0.001$). Thus, while T_S outside of the dung cavities ranged from 50 to 62° C in the 60 observations, inside of the cavities they were ≥40° C in only 10% of the reading and ≥50° C in < 2%. The only two cavities in which T_S was >45° C were the only two in which grasshoppers were not present before the reading was taken.

The lower temperatures and solar radiation loads within the dung cavities correlated with substantially lower operative body temperatures (Fig. 1). The mean operative body temperature of grasshopper models (= dried grasshoppers) placed within shaded dung cavities was 17.5° C lower on average than that of models placed in a standard posture on fully insolated soil surfaces nearby (Wilcoxon test, $P < 0.001$). The equilibrium T_E of the 20 grasshoppers inside dung cavities varied from 33.5 to 40.0° C, while those in full sun ranged from 47.5 to 63.6° C.

Discussion

There have been a number of surveys of dung insect communities, but most have been confined to the early successional stages of decomposition in the month following dung deposition (Duffield 1937; Mohr 1943; Sanders & Dobson 1966; Poorbaugh et al. 1968; Valiela 1969, 1974; Blume 1970, 1972; Wingo et al. 1974; Merritt & Anderson 1977; Schoenly 1983; Hanski & Cambefort 1991). The major coleopteran and dipteran scavengers of dung exploit it soon after it is deposited, when it still has a high moisture content (e.g., Valiela 1974, Wingo et al. 1974, Schoenly 1983). Like termites (Johnson & Whitford 1975) and tenebrionid beetles (Matthews 1976), the grasshoppers that I observed fed on older, drier material. The condition of the droppings corresponded to that described by Mohr (1943) for the period after the major coleopteran and dipteran dung feeders have completed development.

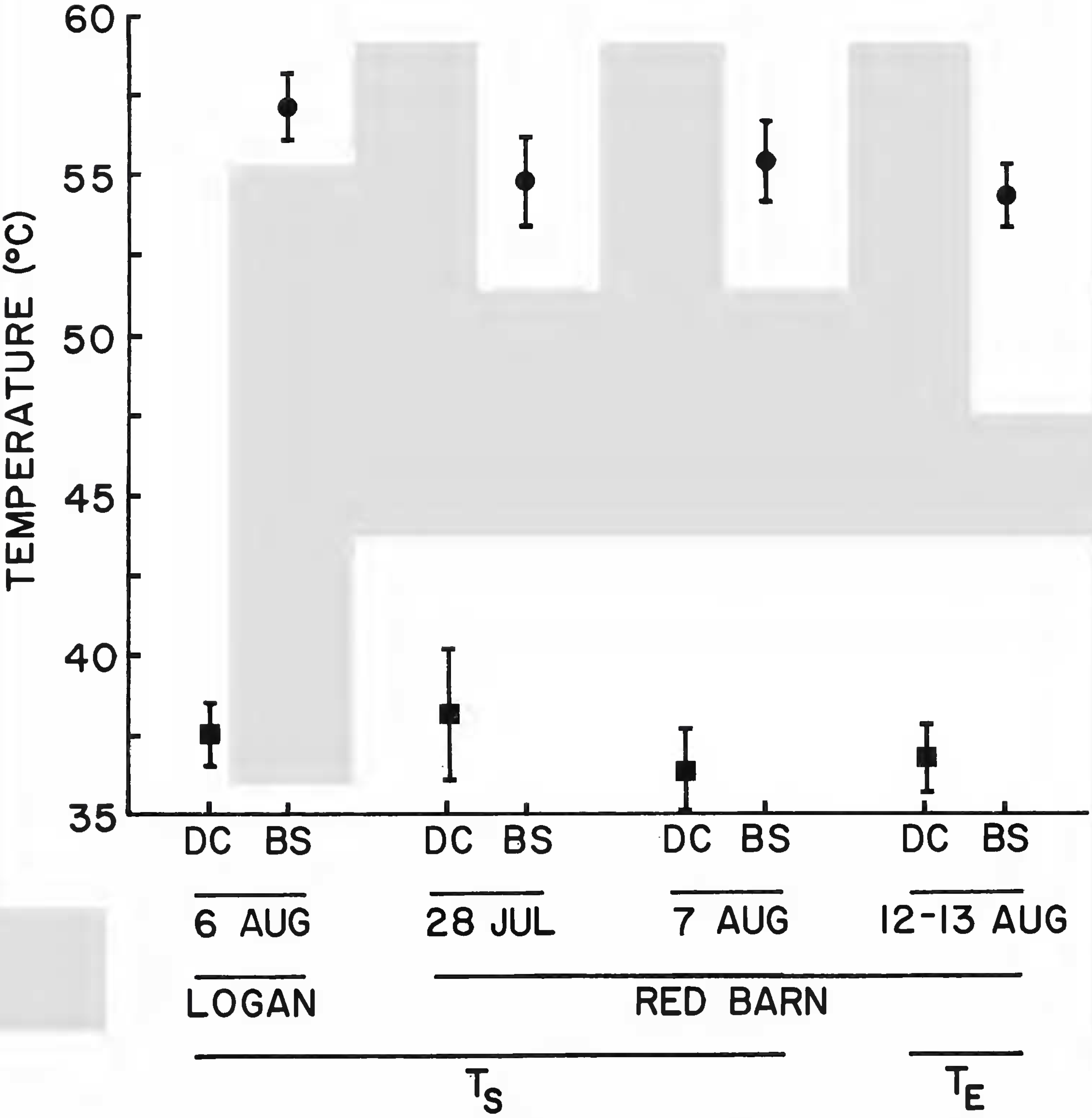

Figure 1. Mean (± 2 SE) soil surface temperatures (T_S) and operative body temperatures (T_E) within dung cavities (DC) and on bare (fully insolated) soil (BS) for different dates and sites ($n = 20$ for all means).

I know of no previous extensive observations on the association of grasshoppers with livestock dung. Lavigne & Pfadt (1964) observed consumption of dried dung by nine species of grasshoppers in Wyoming and Colorado, but provided no other details. Their list included 3 species observed as dung feeders at my sites: *A. coloradus, A. deorum,* and *A. elliotti.* Gangwere (1961) also notes that dung has been reported as grasshopper food, but does not specify the species or the conditions under which scavenging occurs. The propensity for grasshoppers to consume manure was also recognized earlier in this century. A poisoned bait, known as Criddle Mixture and consisting of horse manure laced with insecticide (e.g., arsenic), was used with some effectiveness to control grasshopper outbreaks in Manitoba (Criddle 1920). Rentz (1970) reports observations of a species of *Macrobaenetes* (Orthoptera: Gryllacrididae) feeding on kangaroo-rat and lizard feces.

Dung feeding was observed in all 3 subfamilies of Acrididae present at the research sites (Table 1). With the exception of *Melanoplus packardii* Scudder and *M. sanguinipes,* all of the species of grasshoppers that were observed feeding on dung are classified as either gramnivorous or mixed gramnivorous by Mulkern et al. (1969). Five of the species that I did not observe to feed on dung are not classified as gramnivorous. However, they were either rare at my sites or they occupied different microhabitats. For example, *Dissosteira carolina* (L.) was abundant in weedy roadside vegetation, but uncommon where my observations took place. Furthermore, three of these species (i.e., *Hesperotettix viridis* (Scudder), *Hadrotettix trifasciatus* (Say), and *Xanthippus corralipes* Haldeman) were observed feeding on dried dung by Lavigne & Pfadt (1964). Therefore, the apparent association of preference for grasses with feeding on dung may be an artifact of the low population density of non-gramnivores at my sites. The correlation between abundance of a species and its frequency in the sample of feeders at the red barn site indicates that more exhaustive sampling at the two sites may have lengthened the list of observed feeders.

Studies of possible spatial and temporal variation in the propensity for grasshoppers to feed on dung will be needed to determine how common dung feeding is in grasshopper communities. Interestingly, because of frequent rain during the summer of 1992, the mid- to late-summer vegetation was relatively lush compared with other years. Thus, the grasshoppers fed on dung even though relatively lush vegetation was abundant. Grasshoppers reared on material with a high moisture content are known to prefer dry food when given the choice (Chapman 1990), so desiccated dung may be an attractive alternative food during times of high water availability. An opposite trend may occur in dry years. In 1988, at a nearby site, grasshoppers were observed feeding on fresh cattle dung at an extremely dry and heavily grazed site (J. Holmes, personal communication).

The existence of grasshopper feeding on livestock dung has several possible implications, the significance of which depends on how widespread it is. First, field studies of diet mixing may have to take into account not only the host plants, but other sources of nutrition such as livestock feces and insect cadavers (Lockwood 1988, O'Neill et al. 1993). Many of the species that I have observed feeding on grasshopper cadavers at this site (O'Neill et al. 1993 and unpublished data) were also among the most common dung feeders: *A. elliotti, A. deorum, M. infantilis, M. sanguinipes,* and *S. equale.*

Second, grasshopper diet studies based on crop content analysis (e.g., Mulkern et al. 1969, Gangwere 1961) may not always reflect host plant choice by grasshoppers if some of the material in the gut was derived from dung feeding. This problem is reduced in studies at sites at which domestic grazers were absent (e.g., Joern 1985). However, it is possible that grasshoppers also feed on the excrement of non-domestic herbivores (e.g., ground squirrels, antelope). For example, during the same field season, I observed grasshoppers feeding on grasshopper feces (O'Neill, unpublished data). Third, because desiccation and hardening inhibits microbial decomposition of dung (Merritt & Anderson 1977) grasshoppers may play a valuable role in degradation of older dung piles. By converting large masses of livestock dung into smaller grasshopper feces, both physically- and microbially-mediated rates of decomposition and nutrient cycling could be enhanced.

The observations also suggest that grasshoppers used the cavities they created in dung while feeding to maintain non-lethal or even optimum body temperatures during the hottest periods of the day. Within the shade of cavities, they experienced lower environmental temperatures and lower solar radiation loads. As a result, the operative body temperatures recorded for grasshoppers in dung cavities were well below 1) temperatures they would experience on fully insolated soil surfaces and 2) the known critical thermal maxima for acridids (Chappell & Whitman 1990). The mean T_E (36.7° C, SE = 0.51) measured for the grasshoppers in dung cavities was in the range of preferred temperatures observed for many grasshoppers (Chappell & Whitman 1990). Although dung cavities may be useful as thermal refuges, they are not critical in areas where sufficient standing vegetation is available (as at my sites). Grasshoppers typically use perches on vegetation as a means of lowering mid-day body temperatures via convective heat loss (Chappell & Whitman 1990). However, the thermal properties of the dung cavities did allow grasshoppers to continue feeding on dung even during the hottest periods of the day and may be important in areas were grazing livestock have removed most of the tall vegetation. Furthermore, visually hunting predators such as sparrows (Joern 1988), may also be less likely to find grasshoppers thermoregulating in dung cavities than those perched on plant stems.

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